

# OCCURRENCE OF CRYSTALS IN IRIDACEAE AND ALLIED FAMILIES AND THEIR PHYLOGENETIC SIGNIFICANCE<sup>1</sup>

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## ABSTRACT

Styloid crystals, presumed to be calcium oxalate, seem to be a fundamental characteristic of Iridaceae based on previous reports of their presence in several genera of both major subfamilies, and supplemented here by further records in 75 of the ca. 85 genera of the family. Styloids have now been reported in some 300 species of Iridaceae, of about 320 examined. These elongated crystals are lacking in a few scattered species but perhaps significantly from *Sisyrinchium* and some closely allied genera. Families and isolated genera possibly related to Iridaceae, including *Geosiris* and *Isophysis*, were also examined for crystal types. Styloids are present in *Isophysis*. Tecophilaeaceae and Campynemaceae have raphides and three species of Colchicaceae and several of Uvulariaceae have crystal sand. A few of the latter have raphides, sometimes with crystal sand. Crystals are absent in *Geosiris*. The difference in crystal types taken together with some significant differences in morphology suggest that Campynemaceae and Colchicaceae are not immediately allied either to Iridaceae or to one another. We suggest that Campynemaceae may be better placed close to Melanthiaceae or Burmanniaceae. *Isophysis*, with three stamens but a superior ovary, is probably best treated in its own subfamily of Iridaceae. Tecophilaeaceae are no longer believed to be closely related to Iridaceae and their placement in a different order is supported.

Data on the kinds of crystals of the calcium oxalate type (raphides, styloids, and crystal sand) occurring in plant tissues are widely scattered in the literature and information concerning their distribution in the plant kingdom is not readily available to systematists. Although little is known about the function of such crystals in plants, their shape and location are often very characteristic at different taxonomic levels (Franceschi & Horner, 1980). A brief mention by Metcalfe (1961) that styloids (pseudoraphides) were particularly characteristic of Iridaceae seemed intriguing and worth further investigation to establish, as far as seems reasonable, the frequency of styloids and possibly other crystal types in the family. We have also surveyed the crystal characters in putative relatives of Iridaceae. These include the monotypic Madagascan Geosiridaceae; Colchicaceae (Liliaceae-Colchicoideae); Uvulariaceae (Liliaceae-Uvularioideae); the Tasmanian *Isophysis*; and the poorly known Australasian *Campynema* and *Campynemanthe*. The latter two genera are variously assigned to Hypoxidaceae, Colchicaceae (Dahlgren & Clifford, 1982), or to a separate Campynemaceae (Dumortier, 1829:

57-58; Dahlgren & Rasmussen, 1983) and have been suggested to be close to Iridaceae (Dahlgren & Rasmussen, 1983: 369-372). Uvulariaceae sensu Dahlgren & Rasmussen, postulated as ancestral to Colchicaceae and to Iridaceae (Dahlgren, pers. comm.), comprises *Hexacyrtis* and the *Disporum* group of Liliaceae and is largely North Temperate. A few members of Tecophilaeaceae were also examined because this family was proposed as close to the ancestral line of Iridaceae by Hutchinson (1973), although there is little current support for his view.

## MATERIALS AND METHODS

Dry or FAA-fixed living leaf samples were gathered from at least one to a few species of many genera of Iridaceae from both subfamilies, Iridoideae (here including Sisyrinchioideae) and Ixioideae. Samples were examined at Missouri Botanical Garden (MO) and Royal Botanic Gardens, Kew (K). At MO samples were sometimes cleared in 5% NaOH for several hours or more until satisfactorily transparent or more often were cleared in household bleach. They were then

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mounted immediately in glycerin or dehydrated through an alcohol series and permanently mounted in Canada balsam. At K samples were sectioned using a Reichert sliding microtome. Sections were stained in safranin and alcian blue, dehydrated through an alcohol series and mounted in Euparal. The samples were viewed between polarizing filters to detect the presence and type of crystals in the tissue. The sole species of *Isophysis* and *Geosiris*, one each of *Campynema* and *Campynemanthe* and several of Colchicaceae, Uvulariaceae, Liliaceae (sensu Dahlgren & Clifford, 1982) and Tecophilaeaceae (Table 1) were treated in the same way at MO for comparison. The genera and species studied are listed in Table 1 together with the crystal types observed. Voucher or accession number information is available from the authors but is not reported here.

#### OBSERVATIONS

Slender styloids of the type first described for Iridaceae in *Iris*, *Crocus*, *Romulea*, *Witsenia*, and *Gladiolus* by Gulliver (1863a, 1863b, 1865) and later by Rothert and Zalenski (1899) (see Netolitsky, 1929 for an early review) and in several other genera more recently (see below) were found in the leaves of the majority of species examined but notably not in *Sisyrinchium* and some closely related genera. The styloids are typically long and slender, with pointed or forked ends (Figs. 1, 2, 7) or occasionally square ends (Figs. 3, 4). They are strongly birefringent and vary considerably in size, the length being 100 to 200 (to 300)  $\mu\text{m}$  or sometimes much longer.

In a few species (*Patersonia macrantha*, *P. sericea*, *P. umbrosa*, *Romulea atrandra*) short, more or less isodiametric crystals, 16 to 25  $\mu\text{m}$  long, were observed (Fig. 8) of the type described by de Vos (1970) in *Romulea* and Rudall (1983) in *Diets*. In transverse section styloid crystals appear more or less square (Fig. 6) or rectangular (Fig. 5), occasionally with the longer walls convex. They occur both in the outer vascular bundle sheaths (Fig. 6) where they are difficult to detect in cleared leaves, and in scattered crystal idioblasts in the mesophyll (Fig. 5), usually in the outer chlorenchymatous layers if the leaves are very thick, observed also by de Vos (1970, 1974).

Crystal sand was noted in only two of several species of *Sisyrinchium* examined. This is the only record of crystal sand in Iridaceae.

TABLE 1. Species examined for crystals: st = styloids; cs = crystal sand; rb = raphides; Ca carb = calcium carbonate; x = no crystal inclusions seen. Brackets indicate crystal type observed in some specimens, but not in others.

Campynemaceae	
<i>Campynema linearis</i> Labill.	rb
<i>Campynemanthe viridiflora</i> Baill.	rb
Liliaceae	
<i>Calochortus tiburonense</i> A. J. Hill	x
<i>Erythronium albidum</i> Nutt.	? Ca carb
<i>Lilium canadense</i> L.	? Ca carb
Colchicaceae	
<i>Ornithoglossum</i> sp.	cs
<i>Baeometra uniflora</i> (Jacq.) G. Lewis	cs
<i>Gloriosa carsonii</i> Baker	cs
Uvulariaceae	
<i>Disporum hookeri</i> (Torrey) Nicholson	rb & cs
<i>D. maculatum</i> (Buckley) Britt.	rb & cs
<i>D. sessile</i> Don	cs
<i>Schelhammera pedunculata</i> F. Muell.	x
<i>Streptopus amplexifolius</i> DC.	rb & ? cs
<i>Tricyrtis affinis</i> Makino	? Ca carb
<i>T. latifolia</i> Max.	? Ca carb
<i>Uvularia sessilifolia</i> L.	? cs
Geosiridaceae	
<i>Geosiris aphylla</i> Baill.	x
Tecophilaeaceae	
<i>Cyanella lutea</i> L. f.	rb
<i>Walleria mackenzii</i> Kirk	rb
<i>Cyanastrum cordifolium</i> Oliver	x
Iridaceae-Isophysidoideae	
<i>Isophysis tasmanica</i> (Hook.) T. Moore	x
Iridaceae-Ixioideae	
<i>Anapalina caffra</i> (Ker ex Baker) G. Lewis	st
<i>Anomalesia cunonia</i> (L.) N. E. Brown	st
<i>A. saccata</i> (Klatt) Goldbl.	st
<i>Anomatheca fistulosa</i> (E. Meyer ex Klatt) Goldbl.	x
<i>A. laxa</i> (Thunb.) Goldbl.	st
<i>A. verrucosa</i> (Vogel) Goldbl.	st
<i>A. viridis</i> (Aiton) Goldbl.	st
<i>Antholyza ringens</i> L.	st
<i>Babiana erectifolia</i> G. Lewis	x
<i>B. odorata</i> L. Bolus	st
<i>B. patula</i> N. E. Brown	st
<i>B. stricta</i> Ker	st
<i>B. villosa</i> Ker	st
<i>B. virginea</i> Goldbl.	x
<i>Chasmanthe aethiopica</i> (L.) N. E. Brown	x

TABLE 1. Continued.

<i>C. bicolor</i> (Gasp.) N. E. Brown	st
<i>C. floribunda</i> (Salisb.) N. E. Brown	st
<i>Crococsmia aurea</i> Planch.	st
<i>C. masonorum</i> (L. Bolus) N. E. Brown	st
<i>C. pottsii</i> (Baker) N. E. Brown	st
<i>Crocus asturicus</i> Herbert	st
<i>C. banaticus</i> J. Gay	st
<i>C. cancellatus</i> Herbert	st
<i>C. candidus</i> Clarke	st
<i>C. carpetanus</i> Boiss. & Reut.	st
<i>C. etruscus</i> Parl.	st
<i>C. flavus</i> Weston	st
<i>C. hadriaticus</i> Herbert	st
<i>C. heuffelianus</i> Herbert	st
<i>C. malyi</i> Vis.	st
<i>C. pulchellus</i> Herbert	st
<i>C. speciosus</i> M. Bieb.	st
<i>C. tomasinianus</i> Herbert	st
<i>C. tournefortii</i> J. Gay	st
<i>C. veluchensis</i> Herbert	st
<i>C. vernus</i> Hill	st
<i>Dierama igneum</i> Klatt	st
<i>D. pictum</i> N. E. Brown	st
<i>D. pulcherrimum</i> Baker	st
<i>D. tysonii</i> N. E. Brown	st
<i>Freesia andersoniae</i> L. Bolus	st
<i>F. caryophyllacea</i> (Burm. f.) N. E. Brown	st
<i>F. fergusoniae</i> L. Bolus	st
<i>Geissorhiza aspera</i> Goldbl.	st
<i>G. excapa</i> (Thunb.) Goldbl.	st
<i>G. heterostyla</i> L. Bolus	st
<i>G. inflexa</i> (Delaroche) Ker	st
<i>G. inaequalis</i> L. Bolus.	st
<i>G. longifolia</i> (G. Lewis) Goldbl.	st
<i>Gladiolus carmineus</i> C. H. Wright	st
<i>G. dalenii</i> van Geel	st
<i>G. debilis</i> Ker	st
<i>G. punctulatus</i> Schrank	st
<i>G. scullyi</i> Baker	st
<i>G. segetum</i> Ker	st
<i>G. stellatus</i> G. Lewis	st
<i>G. splendidus</i> Rendle	st
<i>G. watsonioides</i> Baker	st
<i>Hesperantha alpina</i> (Hook. f.) Pax ex Engler	st
<i>H. bachmannii</i> Baker	st
<i>H. falcata</i> (L. f.) Ker	st
<i>H. petitiana</i> (A. Richard) Baker	st
<i>H. radiata</i> (Jacq.) Ker	st
<i>Homoglossum guthriei</i> (L. Bolus) L. Bolus	st
<i>H. muirii</i> (L. Bolus) N. E. Brown	st
<i>H. priorii</i> (N. E. Brown) N. E. Brown	st
<i>Ixia maculata</i> L.	st
<i>I. orientalis</i> L. Bolus	st

TABLE 1. Continued.

<i>Lapeirousia anceps</i> (L. f.) Ker	st
<i>L. bainesii</i> Baker	st
<i>L. coerulea</i> Schinz	st
<i>L. corymbosa</i> (L.) Ker	st
<i>L. divaricata</i> N. E. Brown	st
<i>L. pyramidalis</i> (Lam.) Goldbl.	x
<i>L. rhodesiana</i> N. E. Brown	st
<i>Melasphaerula ramosa</i> (Burm. f.) N. E. Brown	st
<i>Micranthus plantagineus</i> (Pers.) Ecklon	st
<i>Oenostachys dichroa</i> Bullock	st
<i>O. schweinfurthii</i> Baker	st
<i>O. zambeziacus</i> (Baker) Goldbl.	st
<i>Pillansia templemanii</i> (Baker) L. Bolus	st
<i>Radinosophon leptostachya</i> N. E. Brown	st
<i>Romulea atrandra</i> G. Lewis	st
<i>R. bulbocodium</i> Sebast. & Maur.	st
<i>R. flava</i> (Lam.) de Vos	st
<i>R. grandiscapa</i> J. Gay ex Baker	st
<i>R. phoenicea</i> Mouterde	st
<i>R. ramiflora</i> Tenore	st
<i>R. rosea</i> (L.) Ecklon	st
<i>Savannosophon euryphylla</i> (Harms) Goldbl. & Marais	x
<i>Schizostylis coccinea</i> Backh. & Harvey	st
<i>Sparaxis grandiflora</i> (Delaroche) Ker	st
<i>Synnotia variegata</i> Sweet	st
<i>S. villosa</i> (Burm. f.) N. E. Brown	st
<i>Syringodea bicolor</i> Baker	st
<i>Thereianthus lapeirousioides</i> (Baker) G. Lewis	st
<i>T. spicatus</i> (L.) G. Lewis	st
<i>Tritonia crocata</i> (L.) Ker	st
<i>T. flabellifolia</i> (Delaroche) G. Lewis	st
<i>T. florentiae</i> (Marl.) Goldbl.	x
<i>T. laxifolia</i> (Klatt) Benth. ex Baker	st
<i>T. watermeyerii</i> L. Bolus	st
<i>Tritoniopsis parviflora</i> (Jacq.) G. Lewis	st
<i>T. ramosa</i> (Ecklon ex Klatt) G. Lewis	st
<i>Watsonia aletroides</i> (Burm. f.) Ker	st
<i>W. brevifolia</i> Ker	st
<i>W. meriana</i> (L.) Miller	st
<i>W. stenosophon</i> L. Bolus	st
<i>Zygotritonia crocea</i> Stapf	x
Iridaceae-Iridoideae (incl. Sisyrinchioideae)	
<i>Alophia drummondii</i> (Graham) R. Foster	st
<i>Anomalostylus grandis</i> (Kranzl.) R. Foster	x

TABLE 1. Continued.

<i>Aristea alata</i> Baker	st
<i>A. compressa</i> Buchinger	st
<i>A. ensifolia</i> Muir	st
<i>A. lugens</i> (L. f.) Hort.	st
<i>A. macrocarpa</i> G. Lewis	st
<i>A. platycaulis</i> Baker	st
<i>Belamcanda chinensis</i> (L.) DC.	st
<i>Bobartia aphylla</i> (L. f.) Ker	st
<i>B. gracilis</i> Baker	st
<i>Calydorea campestris</i> (Klatt) Baker	st
<i>C. nuda</i> Baker	st
<i>C. xiphioides</i> (Poepp.) Espinosa	st
<i>Cardenanthus tunariensis</i> R. Foster	st
<i>Cardiostigma longispatha</i> (Herbert) Baker	st
<i>Chamelum frigidum</i> (Poepp.) Ravenna	x
<i>Cipura flava</i> Ravenna	st
<i>C. paludosa</i> Aubl.	st
<i>Cypella hauthalii</i> (Kuntze) R. Foster	st
<i>C. herbertii</i> (Lindl.) Herbert	st
<i>C. linearis</i> (H.B.K.) Baker	st
<i>Dietes bicolor</i> (Steud.) Sweet ex Klatt	st
<i>D. flavida</i> Oberm.	(st)
<i>D. robinsoniana</i> (F. Muell.) Klatt	st
<i>Diplarrhena moraea</i> Labill.	st
<i>Eleutherine bulbosa</i> (Miller) Urban	st
<i>Ennealophus euryandrus</i> (Gris.) Ravenna	st
<i>E. foliosus</i> (H.B.K.) Ravenna	st
<i>Fosteria guatemalensis</i> (Standl.) Ravenna	st
<i>F. oaxacana</i> Molseed	st
<i>Galaxia fugacissima</i> (L. f.) Druce	st
<i>Gelasine azurea</i> Herbert	st
<i>G. coerulea</i> (Vell.) Ravenna	st
<i>Herbertia lahue</i> (Molina) Goldbl.	st
<i>H. puchella</i> Sweet	st
<i>Hesperoxiphion peruvianum</i> Baker	st
<i>Homeria collina</i> (Thunb.) Salisb.	st
<i>H. elegans</i> Sweet	st
<i>H. marlothii</i> L. Bolus	st
<i>Iris pumila</i> L.	st
<i>Larentia linearis</i> (H.B.K.) Klatt	st
<i>Libertia caerulescens</i> Kunth & Bouche	st
<i>L. chilensis</i> (Mol.) Gunckel	st
<i>L. elegans</i> Poepp.	st
<i>L. formosa</i> R. Graham	st
<i>L. grandiflora</i> (R. Br.) Sweet	st
<i>L. ixioides</i> (Forst. f.) Sprengel	st
<i>L. paniculata</i> (R. Br.) Sprengel	st
<i>Mastigostyla johnstonii</i> R. Foster	st
<i>Moraea bellendenii</i> (Sweet) N. E. Brown	st
<i>M. fugax</i> (Delaroché) Jacq.	st

TABLE 1. Continued.

<i>M. neopavonia</i> R. Foster	st
<i>M. spathulata</i> (L. f.) Klatt	st
<i>M. tripetala</i> (L. f.) Ker	st
<i>Nemastylis tenuis</i> (Herbert) Baker	st
<i>Neomarica caerulea</i> (Ker) Sprague	st
<i>N. gracilis</i> (Herbert) Sprague	st
<i>N. heloysa-mariae</i> P. Och.	st
<i>N. northiana</i> (Schneev.) Sprague	st
<i>Nivenia corymbosa</i> (Ker) Baker	st
<i>N. stokoei</i> N. E. Brown	st
<i>Ona obscura</i> (Cav.) Ravenna	x
<i>Orthrosanthus chimboracensis</i> (H.B.K.) Baker	(st)
<i>O. laxus</i> (Endl.) Benth.	(st)
<i>O. multiflorus</i> Sweet	st
<i>O. polystachyus</i> Benth.	st
<i>Patersonia fragilis</i> (Labill.) Asch. & Graeb.	st
<i>P. glabrata</i> R. Br.	st
<i>P. graminea</i> Benth.	st
<i>P. juncea</i> Lindl.	st
<i>P. longiscapa</i> Sweet	(st)
<i>P. lowii</i> Stapf	st
<i>P. macrantha</i> Benth.	st
<i>P. occidentalis</i> R. Br.	st
<i>P. novoguineensis</i> L. S. Gibbs	st
<i>P. pygmaea</i> Lindl.	st
<i>P. sericea</i> R. Br.	st
<i>P. umbrosa</i> Endl.	st
<i>Phaiophleps biflora</i> (Thunb.) R. Foster	x
<i>Pseudotrimezia barretoii</i> R. Foster	st
<i>Sessilanthera citrina</i> Cruden	st
<i>S. heliantha</i> (Ravenna) Cruden	st
<i>Sisyrinchium acre</i> Mann.	x
<i>S. alatum</i> Hook.	x
<i>S. angustifolium</i> Miller	x
<i>S. cuspidatum</i> Poepp.	x
<i>S. chilense</i> Hook.	x
<i>S. elmeri</i> Greene	x
<i>S. fasciculatum</i> Kl.	cs
<i>S. filifolium</i> Gaudich	x
<i>S. grandiflorum</i> Dougl. ex Lindl.	x
<i>S. idahoense</i> Bicknell	x
<i>S. junceum</i> E. Meyer	x
<i>S. longipes</i> (Bickn.) Kearney & Peebles	x
<i>S. macrocarpum</i> Hier.	x
<i>S. micranthum</i> Cav.	x
<i>S. nashii</i> Bickn.	st
<i>S. pachyrhizum</i> Baker	x
<i>S. setaceum</i> Kl.	?x
<i>S. striatum</i> Sm.	x
<i>S. tinctorum</i> H.B.K.	x
<i>S. vaginatum</i> Spreng.	cs
<i>Solenomelus sisyrinchium</i> (Gris.) Pax ex Diels	st

TABLE 1. Continued.

<i>S. pedunculatus</i> (Gill.) Johnston	st
<i>Sphenostigma mexicanum</i> R. Foster	st
<i>S. sellowianum</i> (Klatt) Baker	st
<i>Tapeinia pumila</i> (Forst. f.) Baill.	st
<i>Tigridia bicolor</i> Molseed	st
<i>T. dugesii</i> S. Wats.	st
<i>T. huajuapense</i> Molseed ex Cruden	st
<i>T. meleagris</i> (Lindley) Nichols.	st
<i>T. pavonia</i> (L. f.) DC.	st
<i>T. orthantha</i> (Lemaire) Ravenna	st
<i>T. seleriana</i> (Loesener) Ravenna	st
<i>Trimezia martii</i> (Baker) R. Foster	st
<i>T. martinicensis</i> (Jacq.) Herbert	st
<i>T. sincorana</i> Ravenna	st
<i>T. steyermarkii</i> R. Foster	st
<i>Witsenia maura</i> Thunb.	st

The unusual Tasmanian relict *Isophysis*, often associated with Iridaceae because of its equitant leaves and three stamens, but a superior ovary, also has styloids, although not in all specimens examined.

In contrast, *Campynema* and *Campynermanthe* have typical raphides and no styloids. Members of Colchicaceae examined lack true raphides but have crystal sand. Crystal sand (described by Netolitsky, 1929) consists of small and scattered globose to ovoid birefringent granules. Uvulariaceae are heterogeneous for crystals. Two species of *Disporum* and one of *Streptopus* have both raphides and crystal sand, while a third species of *Disporum* has crystal sand only. A single species of *Uvularia* examined has a few scattered crystals that may be crystal sand and in *Schelhammera* we found no crystalline inclusions at all. The two species of *Tricyrtis* and the single species each of *Erythronium* and *Lilium* (both Liliaceae) studied here, have what appear to be large round crystals of calcium carbonate (the tissue bubbles in bleach and even more when dilute hydrochloric acid is added). No crystals were seen in *Calochortus*.

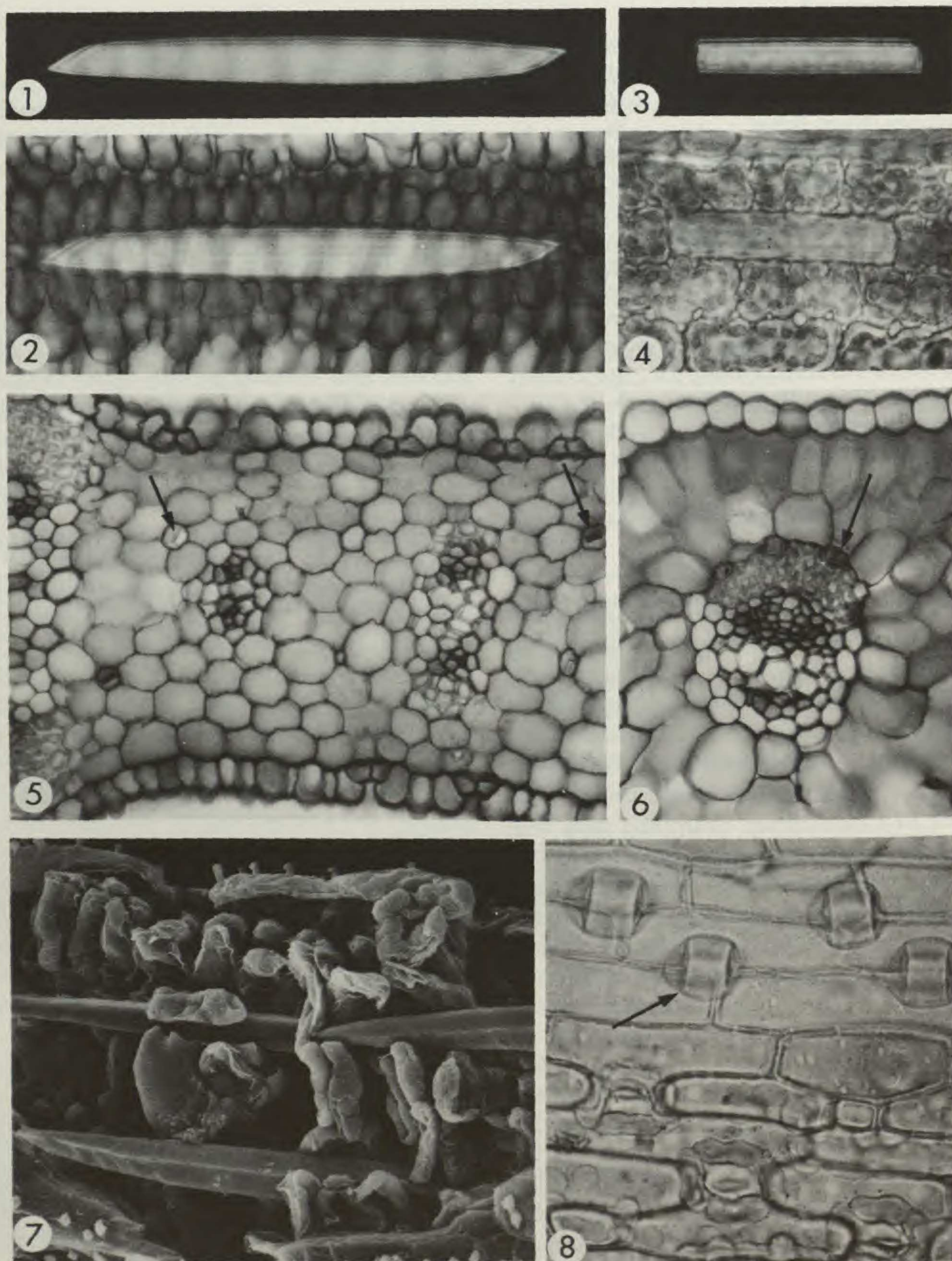
No crystals of any kind were detected in *Geosiris* but because this monotypic genus is a non-green leafless saprophyte the comparison of its leaf scales with the green fully developed leaves of other species may not be valid.

Raphides were noted in *Cyanella* and *Walleria* (Tecophilaeaceae) but no crystals of any sort were seen in *Cyanastrum*, a genus often treated as a separate family, Cyanastraceae.

## DISCUSSION

The occurrence of styloids already noted by Metcalfe (1961), Hegnauer (1963), Gibbs (1974), and others to be a peculiarity of Iridaceae, appears to be a fundamental and nearly universal characteristic of the family on the basis of a survey here of some 240 species in 75 genera. Our data supplements previous reports of styloids in the Ixioid genera *Crocus*, *Romulea*, and *Gladiolus* (Gulliver, 1863a, 1863b; Rothert & Zalenski, 1899) and in *Romulea*, *Syringodea*, *Homoglossum*, and *Tritonia* (de Vos, 1970, 1974, 1976, 1982: 30). In Iridoideae, styloids have been described in a few genera including *Iris*, *Witsenia*, and *Belamcanda* (Gulliver, 1863a, 1863b; Rothert & Zalenski, 1899; Frey, 1929; Wu & Cutler, in press), *Ferraria* (de Vos, 1979), and *Dietes* (Rudall, 1983). Styloids were described by Noel (1959) in *Bobartia* (also Iridoideae) (and possibly by Strid, 1974: 10–12 who observed square crystals in sectioned leaves). Chodat and Balicka-Iwanowska (1892) observed large styloids arranged longitudinally and surrounding vascular bundles in the leaves of many genera of Iridaceae. The absence of styloids in *Sisyrinchium* leaves was first noted by Gulliver (1865) in *S. anceps*, *S. striatum*, and *S. bermudianum* and later by Rothert and Zalenski (1899) in *S. bermudianum*, and confirmed in 20 out of 21 species in this study. The lack of styloids in *Sisyrinchium* and also the closely related genera *Phaiophleps* and *Chamelum* may well have some significance for the systematics of those genera, although styloids do occur in *Libertia* and *Tapeinia*, also close to this alliance. Rudall (in press) also found styloids completely lacking in rhizomes of *Sisyrinchium*, whereas they are present in underground stems of most genera of Iridaceae. Apart from this, the occasional absence of styloids in a few scattered species appears to have no systematic relevance. The size and shape of crystals in Iridaceae is also somewhat variable. The occurrence of cuboidal crystals (Fig. 8) in a few species has little obvious taxonomic significance; crystal shape may depend to some extent on the shape of the crystal idioblast enclosing it (Franceschi & Horner, 1980). However, Wu and Cutler (in press) have found that styloid shape and size in *Iris* may well be taxonomically useful at the species level.

Styloids are relatively rare in the monocotyledons but are also characteristic of Agavaceae, Phormiaceae, and a few other families or sub-



FIGURES 1-8. Crystals in Iridaceae.—1, 2. *Trimezia sincorana*, crystal with pointed ends in LS leaf. (1. Polarized. 2. Bright field).  $\times 700$ .—3, 4. *Patersonia longiscapa*, crystal with square ends in LS leaf. (3. Polarized. 4. Bright field).  $\times 700$ .—5. *Gladiolus daleni*, leaf TS. Crystals (arrowed) in scattered mesophyll cells.  $\times 630$ .—6. *Crocus cancellatus*, leaf TS. Crystals (arrowed) in vascular bundle sheath.  $\times 650$ .—7. *Geissorhiza aspera*, scanning electron micrograph. Crystals among mesophyll cells.  $\times 500$ .—8. *Patersonia umbrosa*, leaf surface, showing cuboidal crystals (arrowed) immediately beneath epidermis, over veins.  $\times 1,400$ .

families of Asparagales (Dahlgren & Clifford, 1982: 92). They have not, however, been recorded in any members of Liliales sensu stricto except Iridaceae.

The discovery of raphides in Campynemaceae appears to be the first report for the family and crystal sand appears not to have been recorded previously in Colchicaceae. Genera of Colchi-

caceae have long been known to lack raphides or styloids (Hegnauer, 1963; Gibbs, 1974). In Uvulariaceae, data for *Uvularia* are contradictory, Hegnauer reporting raphides here but both Gibbs (1974: 1915) and Sterling (1977) point out their absence, a condition we confirm. The few examples of the Uvulariaceae we examined indicate that the alliance as circumscribed to include *Tricyrtis*, and the *Disporum-Uvularia* group of genera, is heterogeneous for crystal types. Either raphides and scattered crystal sand occur (*Streptopus*, *Disporum*) or crystal sand alone (*Uvularia*, *Disporum*) or no calcium oxalate type crystals at all (*Schelhammera*, *Tricyrtis*) but possibly calcium carbonate in *Tricyrtis*. Gibbs (1974: 1915) has also reported raphides in *Streptopus*. The single species each of *Erythronium* and *Lilium* (both Liliaceae) studied here, also have what appear to be large round crystals of calcium carbonate.

The different crystal types found in Colchicaceae, Uvulariaceae, and Campynemaceae contribute little to our understanding of their relationships to Iridaceae but in our view, do constitute evidence for the continued separation of *Campynema* and *Campynemanthe* from Iridaceae. In general raphides may be considered a primitive feature in flowering plant groups (Tomlinson, 1962). The presence of styloids or crystal sand is rare and presumably derived and the styloids of Iridaceae are consistent with the specialized position of Iridaceae in Liliales.

The character of an inferior ovary in Campynemaceae presumably evolved independently in this family and in Iridaceae. Campynemaceae also differ from Iridaceae in the basic leaf form, having bifacial rather than monofacial equitant leaves, and in having six stamens. *Campynemanthe* also has a distinctive type of axile placentation in which the seeds remain attached to the vasculature of the central axis after dehiscence or disintegration of the capsule.

*Isophysis* shares with Iridaceae not only the peculiar but not unique character of monofacial and equitant leaves and an androecium of three stamens, but also the distinctive styloids that appear fundamental in the family. It differs notably from Iridaceae only in having a superior ovary. Early reports that the stamens of *Isophysis* are opposite the inner tepals (Bentham & Hooker, 1883) and hence not comparable with Iridaceae are incorrect. We have examined the limited material available to us and confirm the

statement by Krause (1930: 260) that the stamens are opposite the outer tepals. It now seems desirable to include *Isophysis* in Iridaceae on the grounds mentioned above but it should probably be treated as a separate rather isolated subfamily, whose affinities to the other subfamilies are distant.

Similarities between Colchicaceae and Iridaceae, except for unspecialized characteristics shared with other families of the Liliales, seem restricted to the presence of a cormous rootstock in both families (Dahlgren & Rasmussen, 1983). However, we believe that it is very likely that a rhizome is the basic type of rootstock for Iridaceae and that corms evolved at least twice in the family. In Ixioideae, the corm is basal rooting and has a stele, whereas in some specialized Iridoideae (the predominantly African Homerinae) it is apically rooting and without a stele (de Vos, 1977; Goldblatt, 1976, 1982). Rhizomes occur in many genera of Iridoideae including those with predominantly unspecialized characteristics, several of which are often treated as a separate subfamily Sisyrinchioideae. We are uncertain whether the corm is basic in Colchicaceae, but its structure seems somewhat different from that of the corm types found in Iridaceae and, given our hypothesis that a rhizome is basic in Iridaceae, the presence of corms in other families appears irrelevant in questions of phylogenetic relationship. The absence of styloids and the presence of crystal sand in Colchicaceae seems to remove this family even further from a possible close affinity with Iridaceae. Dahlgren's suggestion (pers. comm.) that Colchicaceae and Iridaceae may be independently derived from Uvulariaceae has merit although it is more difficult to see similarities with Iridaceae than Colchicaceae. In this connection it seems significant that Uvulariaceae is heterogeneous for crystals and provides a possible link between ancestors with the primitive condition of raphides alone and derived lines with specialized crystal types.

Although Tecophilaeaceae are not seriously considered to be allied to Iridaceae, and have been assigned to Asparagales by Dahlgren and Clifford (1982) rather than Liliales, the family was included in this study. The finding of typical raphides, very common in Asparagales, is consistent with their placement in this order on the basis of their phytomelan encrusted seeds and introrse anthers. The absence of any crystals in *Cyanastrum*, already recorded by Dahlgren and

Clifford, in contrast to *Cyanella* and *Walleria*, lends some support to its treatment as a separate family, for example by Dahlgren and Clifford.

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